Landscape effects on bumble bee (Hymenoptera: Apidae) colony performance and fitness in New York State

A thesis

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Master of Science

By

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ABSTRACT

Pollinators such as bumble bees are in decline as a result of many factors, including loss of habitat. Initiatives to improve and restore pollinator habitat have become increasingly popular. However, to most effectively conserve pollinators, we need a better understanding of which habitats are limiting to their survival and growth at the landscape scale. Our study examined the performance of the common eastern bumble bee, *Bombus impatiens* (Cresson), in four common landscapes (natural, suburban, conventional agriculture, and organic agriculture). In the summers of 2016 and 2017, 64 commercial bumble bee colonies were deployed across 16 sites (4 in each landscape) and their growth (weight and bee abundance) and fitness (caste production), and survival were monitored weekly. Across both years, colonies in suburban landscapes were approximately 28-30% lighter, had 13-15% less bee abundance, produced 38-40% fewer worker cells, and 45-50% fewer drones cells. Colonies in suburban landscapes also experienced queen death at a rate two-times faster. In 2016, 100% of the colonies in suburban landscapes were removed due to queen death, which was six days earlier than the overall average across all landscapes. In 2017, over 50% of the suburban colonies had queens die before the overall average across all landscapes. Our study adds to the growing literature highlighting the influence of the landscape context on pollinator populations, particularly in suburban environments. Overall, our results suggest that suburban landscapes are suboptimal for *B. impatiens* while agricultural landscapes were not detrimental to colony growth or survival. Future research is needed to identify mechanisms that are responsible for the reduced performance of bumble bee colonies in suburban landscapes, especially regarding floral resources, pesticides, and pathogens.

BIOGRAPHICAL SKETCH

Nelson Milano was born on November 4th in 1989 in Springfield, MA. Whether it was in Springfield or in Puerto Rico, Nelson spent much of his childhood outdoors learning about the various plants and arthropods he encountered. In college, he majored in Science and Biology and became quite invested in the University of Massachusetts – Amherst Entomology department early in his undergraduate career working as a curatorial assistant of the insect collections. This initiated his interest in the study of insects and unexpectedly paved the way for greater opportunities within the Entomology department. In 2014, Nelson joined the McArt lab at Cornell University to work as a lab manager. After a couple of years, he joined the Department of Entomology as a MS student for the 2016 academic year to study the effects of landscapes and farm practices on the performance of the common eastern bumble bee, *Bombus impatiens*.

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We thank David Lewis, Trebor Hall, and Ashley Fersch with help in setting up the study and fieldwork. Heather Grab, Katja Poveda, and Cornell Statistical Consulting Unit for guidance with statistical analyses. Susan Earle, Kathy Albertini, Mellissa Fierke, Greg Loeb, Chuck Guard, Larry Smart, Brian Shiels, Bill Wickham, Andrew Fellenz, Jamie Eldenstein, David Fox, JoAnn Delaney, Ammie Chickering, Bob Tuori, Finger Lakes Land Trust, Genesee Land Trust, Central NY Land Trust, and the city of Geneva, NY for allowing use of their properties to conduct this study.

LIST OF FIGURES

Figure 1: Average percent land composition 5

Figure 2: Mean colony weight 9

Figure 3: Mean bee abundance 11

Figure 4: Mean worker cell abundance.....12

Figure 5: Mean drone cell abundance.....13

Figure 6: Virgin queen cell production.....14

Figure 7: Colony survival 15

Figure 8: Correlations between relative colony growth and percent developed land and impervious surface.....16

TABLE OF CONTENTS

Biographical sketch iii

Acknowledgements iv

List of Figures v

Landscape effects on bumble bee (Hymenoptera: Apidae) colony performance and fitness in New York State 1

Introduction 1

Materials and Methods 3

Study System 3

Field sites and colony placement 5

Colony performance 6

Statistical analysis 7

Results 8

Colony performance 9

Colony fitness and survival 13

Predictors of colony performance, fitness and survival 16

Discussion 18

Introduction

Wild pollinators in both Europe and North America have been experiencing population declines and range contractions (Biesmeijer et al. 2006, Potts et al. 2010, Cameron et al. 2011). Given that pollinator species contribute to the reproduction of approximately 60-70% of wild and cultivated plant species, their declines do not only impact human global food security, but also the communities of organisms that rely on the fruits and seeds produced from pollination (Klein et al. 2007, Garibaldi et al. 2011, Burkle et al. 2013, Vanbergen et al. 2013). Recent research has identified factors associated with declines in wild bee populations, including exposure to pesticides, parasites, and lack of floral resources (Kosior et al. 2007, Williams and Osborne 2009, Cameron et al. 2011, Bartomeus et al. 2013, Goulson et al. 2015, McArt et al. 2017). Habitat degradation and loss from urbanization and agricultural intensification are often cited as major drivers of declines (Williams and Kremen 2007, Winfree et al. 2011, Williams et al. 2012), yet comparative studies assessing how bees perform across multiple impacted landscapes are rare. Such information is critical to inform effective conservation efforts.

The urban landscape is rapidly expanding. Fifty-four percent of the world population lives in urban areas, and it is projected to increase by 12% by the year 2030 (United Nations Populations Fund 2007). For pollinators, urban expansion results in habitat loss or fragmentation, which in turn can reduce the availability of forage and nesting substrates needed to persist (McIntyre and Hostetler 2001, Johnson and Klemens 2005). Pollinator diversity and abundance for solitary bee species tend to decrease with increasing urbanization in both cities and suburbs (Hernandez et al. 2009, Bates et al. 2011, Fortel et al. 2014). However, not all urban landscapes are alike, and some taxa may respond differently to urbanization. *Bombus terrestris* has recently been found to perform better in urban landscapes compared with agricultural landscapes in the

United Kingdom (Samuelson et al. 2018). Similarly, related bumble bee species visiting suburban garden beds in the United Kingdom had longer lifespans (Goulson et al. 2010) grew much faster, and grew larger than colonies in agricultural landscapes (Goulson et al. 2002). In North America, bumble bees have been shown to have greater mean abundance in urban parks containing natural land in San Francisco compared with surrounding natural habitats (McFrederick and LeBuhn 2006). Conversely, Glaum et al. (2017) found that diversity and abundance of common northeastern U.S. bumble bees decreased with increased urban landscape when measured in relation to their typical flight distances. In North America, we are aware of only one study that has attempted to examine the effects of urbanization on bumble bee performance (Vaidya et al. 2018).

Agricultural intensification generally has a negative relationship with pollinator diversity and abundance via reduced and/or monotonous forage and reduction of nesting habitats (Scheper et al. 2013, Connelly et al. 2015). Conversely, pollinator diversity and abundance can increase in fields where more of the surrounding landscape is composed of natural habitat (Holzschuh et al. 2012) and where they are closer to surrounding natural lands (Joshi et al. 2016, Kammerer et al. 2016). Furthermore, farm practices in agricultural landscapes can impact pollinators. For example, conventional and organic agricultural practices can expose pollinators to an array of pesticides that may elevate their susceptibility to parasite infection (Baron et al. 2014, David et al. 2016, Botías et al. 2017) which is associated with range contractions in United States bumble bees (McArt et al. 2017). In many cases, organic farms will have a more heterogenous landscape context, allowing for more diverse diets (Rundlöf et al. 2008, Tuck et al. 2014, Schellhorn et al. 2015). Crone and Williams (2016) showed that in relation to floral resources, bumble bee queen production was greatest in natural habitats, intermediate on organic farms, and lowest in

conventional farms. However, a colony's success in a natural habitat is highly dependent on local floral abundance than natural landscape alone (Spiesman et al. 2017). Exceptions in agriculture have included monocultures of mass-flowering crops such as oilseed rape and red clover where early bumble bee colony growth and densities of all caste members significantly increased (Westphal et al. 2009, Rundlöf et al. 2014, but see Rundlöf et al. 2015). More research is clearly needed to differentiate how conventional and organic farm practices in agricultural landscapes impact populations of bumble bee species.

Here, we examine the effects of commonly encountered landscapes on colony performance and survival of the common eastern bumble bee, *Bombus impatiens* (Cresson). Experimental *B. impatiens* colonies were placed in natural, suburban, conventional agriculture, and organic agriculture landscapes in two successive years (2016 and 2017) to address the following questions about *B. impatiens* colony success: 1) How do landscapes and farm practices influence colony growth and survival? and 2) How do landscapes and farm practices influence colony reproductive fitness? We hypothesized that survival and fitness of *B. impatiens* would be greatest in natural and suburban landscapes, followed by organic and conventional agricultural landscapes.

Materials and Methods

Study system

Bombus impatiens is a widely encountered bumble bee species across eastern North America that is active from April to October (Williams et al. 2014). *Bombus impatiens* nests underground, often using old rodent cavities for their hives (Michener 2000). Colonies on average reach a peak size of approximately 400 workers and will switch to producing reproductives (queens and drones) towards the end of their lifecycle (Cnaani et al. 2002). Unlike

many bumble bee species, the status of *B. impatiens* is stable, and it is not a species of conservation concern on the International Union for Conservation of Nature and Natural Resources Red List of Threatened Species (IUCN Red List; Hatfield et al. 2014). However, because *B. impatiens* can thrive in multiple habitats, it can be used as a model organism to determine how the surrounding environment may influence the population growth and fitness of similar species.

In agriculture, *B. impatiens* colonies are available commercially for greenhouse pollination of tomatoes *(Solanum lycopersicum*, L) and supplemental field pollination of cucurbit crops (*Cucurbita pepo,* L.), blueberries (low and highbush; *Vaccinium augustifolium,* Ait.; *Vaccinium* corymbosum, L.), and cranberries (*Vaccinium macrocarpon*, Ait.) (Stubbs and Drummond 2001, Artz and Nault 2011). Research on cucurbits has shown that supplemental colonies of *B. impatiens* transfer more pollen to stigmas, come in contact with the stigmas more often, and require fewer visits to female flowers to achieve large fruit than supplemental hives of *Apis mellifera* (European honey bee, L.) and natural populations of the native specialist, *Peponapis pruinosa* (squash bee, Say) (Artz and Nault 2011). Despite their efficiency, supplemental colonies of *B. impatiens* in cucurbit fields do not improve yield (Petersen et al. 2013, Petersen et al. 2014).

In late June 2016 and 2017, we obtained commercially-reared *B. impatiens* colonies from BioBest Canada Ltd. (Leamington, ON, Canada). Upon arrival, colonies were weighed (nearest 0.1 g) and assessed for numbers of workers, worker cells, and drone cells. Colonies were then grouped according to size (i.e. weight). We replaced the supplied colony covers with 203 x 254mm clear polycarbonate sheets (Lexan; SABIC Innovative Plastics US; Houston, TX) that had drilled ventilation holes (2mm diameter) and a covered access hole (50mm diameter) in the

center. We then placed colonies in corrugated plastic boxes (each containing two colonies) that had the entrances painted (black, blue, pink or yellow) to reduce drift of bees among colonies (Birmingham et al. 2011, Zanette et al. 2014). Prior to deployment, the sugar bladders were removed to ensure that bees would leave the colony and forage.

Field sites and colony placement

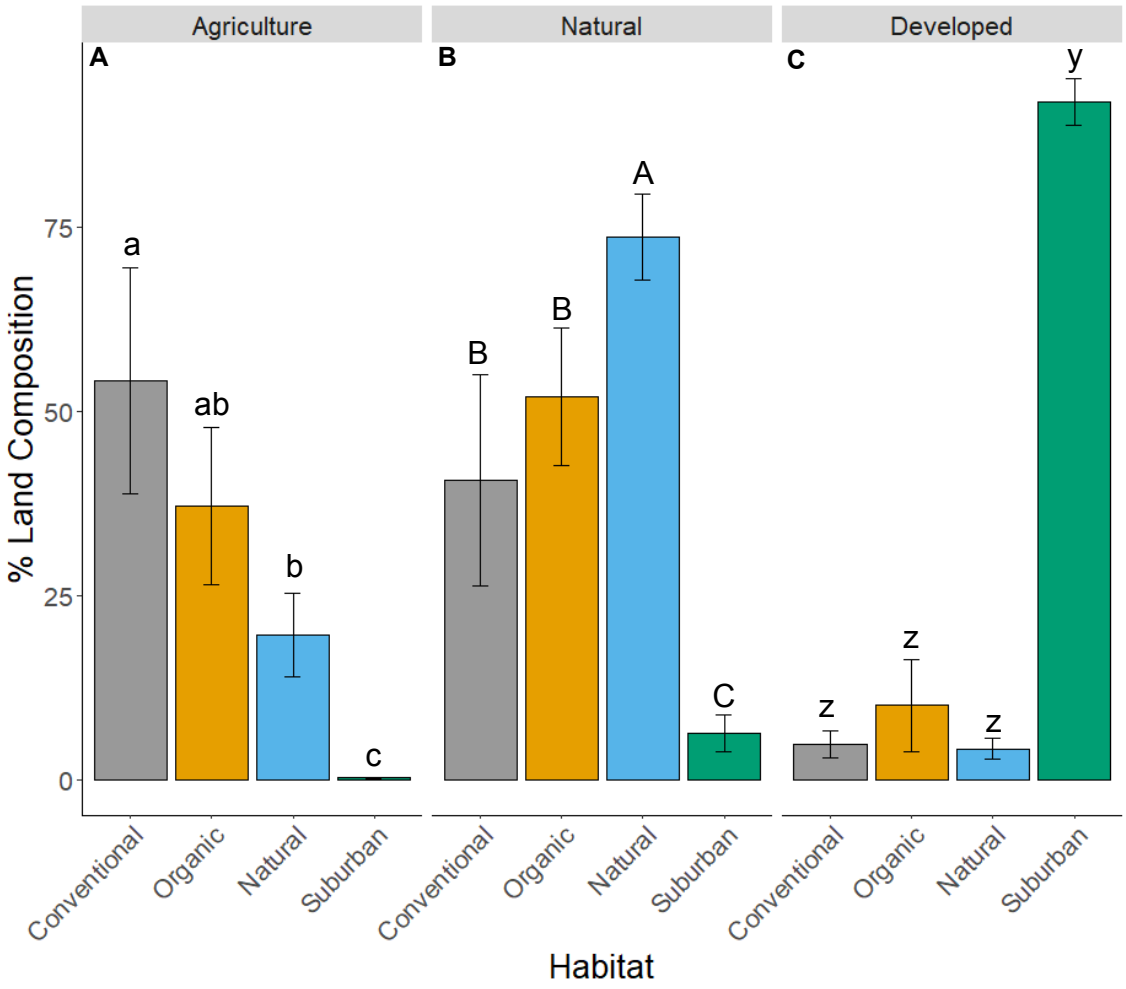

Figure 1: Average percent land composition (+/-SE) at all landscape types at a 800m radius for (A) agricultural land, (B) natural land, (C) developed land. Letters indicate significant differences between landscapes based on post-hoc tests.

Colonies were randomly assigned to one of four landscape types (natural, suburban, conventional agriculture, and organic agriculture). Each landscape type was replicated in regions in proximity to Rochester, Syracuse, Ithaca, and Geneva, NY, USA for a total of four replications and a total of 16 sites (Table S1). Four *B. impatiens* colonies were included at each site for a total of 64 colonies per year. Colonies placed in conventional agriculture and organic agriculture landscapes were positioned in the margins of cucurbit crop fields (e.g., squash and pumpkin) and deployed coinciding with bloom. All colonies were deployed across four days, visiting four sites per region (one for each landscape) between the hours of 09:00-18:00 (July 01-04, 2016 and July 03-06, 2017). In 2017, one natural landscape replicate was lost due to flooding during the first week of assessments and the natural landscape for Geneva was moved to a more appropriate location (Table S1)

All sites were assessed using Geographic Information System (ArcGIS version 10.5.1; ESRI (2018)) and the United States Department of Agriculture Crop Data Layer (CDL; USDA National Agriculture Statistics Service 2016) to determine degree of agricultural, natural and developed land at an 800 m buffer (mean flying radius for bumble bees; see McArt et al. (2017)) (Figure: 1A, B and C). We chose cucurbits to be the most consistent crop across all agricultural landscapes because *B. impatiens* is an important pollinator for this crop. Both organic and conventional agricultural habitats were selected to have a similar field size (range 0.83-5.0 ha) and crop production type (i.e. small to medium mixed vegetable farms). Conventional farms often grew cucurbit crops, corn, and soybeans while organic farms were more diverse, growing cucurbit crops, leafy greens, solanaceous crops, carrots, and onions. The CDL classes for all agricultural crops were summed and percent land composition determined for conventional and organic sites (Figure: 1A, 21-42% land cover at 800 m radius). The area of natural landscape was

calculated by summing the area of all CDL classes that included landcovers relating to grass/pasture, shrubland, wetlands, and forest (Figure: 1B, 61-88% land cover of 'natural' sites at 800 m radius). The area of suburban landscape was calculated by summing the area of CDL classes that were categorized as developed, including low, medium, and high intensity (Figure: 1C, 86-100% land cover of 'suburban' sites at 800 m radius). Additionally, the percent of impervious surfaces in suburban sites was calculated using the National Land Cover Database Percent Developed Imperviousness layer (Xian et al. 2011).

Colony performance

Colony growth and reproductive success metrics were assessed weekly by recording colony weight, bee abundance, brood cell abundance, and gyne abundance during the daylight hours (09:00-18:30 to comply with home/landowner restrictions). Brood cell abundance included counts for worker cells, drone cells, and virgin queen cells, which can be differentiated by shape and size. Colony weight, bee abundance, brood cell abundance, and gyne abundance were averaged across all four colonies at each site. Once the queen from a colony died, the colony was removed from the site, frozen at -20º C and then dissected for final assessment. We used queen death as a proxy for colony survival. Weekly assessments were more reliable than final assessments (i.e. when dead colonies were brought back to the lab and inspected) since old brood cells and honey pots would either be recycled/destroyed by workers or consumed by various pests that eventually invaded the colonies (i.e., Coleoptera: Nitidulidae, Staphylinidae, Sylphidae; Blattodea: Ectobiidae; Diptera: Calliphoridae, Drosophilidae, Muscidae, Phoridae; Lepidoptera: Pyralidae). Therefore, final assessments were not included in the performance and fitness analyses. Relative colony weight was assessed from assessment period one-four (when colonies experienced the greatest growth at most landscapes) in both 2016 and 2017.

Statistical analysis

All statistical analyses were conducted using R (R Core Team 2017), using the lmer4, glmmTMB, survival, coxme, emmeans, ggplot2, ggpuber and survminer packages (Wickham and Chang 2016, Therneau and Lumley 2017, Kassambara 2018, Kassambara et al. 2018, Lenth et al. 2018, Magnusson et al. 2018, Therneau 2018). Models were selected using the lowest AIC scores from likelihood ratio tests (Johnson and Omland 2004). To analyze mean colony weight change, mean bee abundance, mean worker cell abundance, and mean drone cell abundance throughout the duration of the study for both 2016 and 2017, linear mixed effects models were used with "landscape", "year", and "assessment period" as fixed effects and "region" and "site" as random effects. To analyze mean virgin queen cell abundance and mean gyne abundance, we used truncated negative binomial hurdle models with mixed effects because of the excess of zeros in the data. Mean virgin queen abundance and mean gyne abundance were each modeled as a binary process for presence/absence, and the fitting of a truncated negative binomial model with mean counts equal or greater than zero at each site. Models included "landscape" and "year" as fixed effects and "region" and "site" as random effects ("assessment period" was removed as a fixed effect due to insufficient replication). Colony mortality (queen death) was analyzed using Kaplan-Meir survival curves and mixed effects Cox proportional hazard models with "landscape" and "year" as fixed factors and "region" and "site" as random factors. Post-hoc tests for linear mixed effects and survival analyses models were conducted using the Emmeans package (Lenth et al. 2018) adjusted to Tukey's HSD to determine differences between landscape types, year and assessment periods. We analyzed predictors of performance using linear regressions with Pearson correlation coefficients.

Results

Colony performance

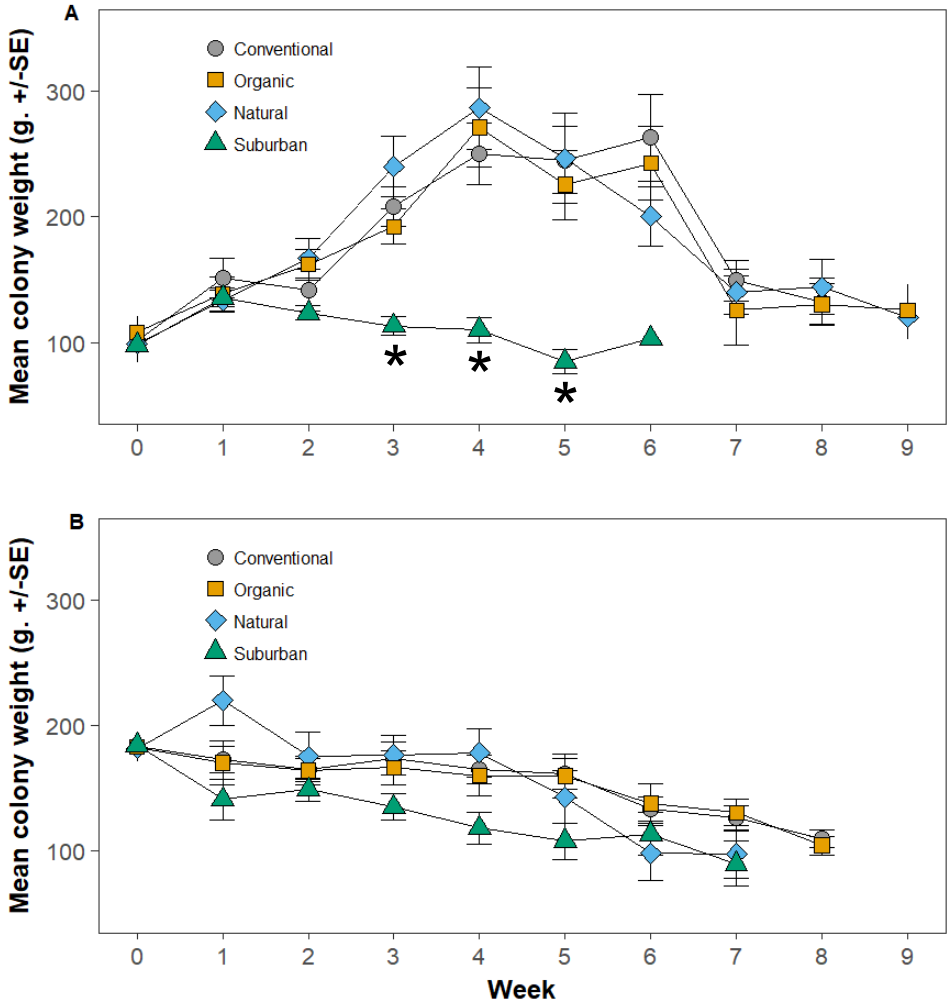

Figure 2: Mean colony weight (g. +/- SE) in (A) 2016 and (B) 2017 of *B. impatiens* colonies placed in agricultural, natural and suburban landscapes. Asterisks indicate significant differences between landscapes based on post-hoc tests of lme models. Assessment weeks 0-9 in 2016 correspond to julian dates 180-252 and assessment weeks 0-8 in 2017 correspond to julian dates 178-256.

Weight – In 2016, we received colonies at a mean weight of 101.5 +/- 24.7 grams (mean +/- SD). By the first assessment period, colonies in all landscapes grew by approximately 28%. However, colonies placed in suburban landscapes only peaked at assessment period one and continued to decline until their full removal from the study at assessment period six. Agricultural and natural landscape colonies peaked at assessment period four and grew approximately 60-

65% in weight compared to their initial weight. In 2017, we received colonies that were approximately 44.8% heavier than colonies in 2016 with a mean colony weight of 183.2 +/- 19.5 grams (mean +/- SD). Only natural landscape colonies grew by 17% in assessment period one while the other landscape decreased by approximately 5-23%.

We found no overall significant effect of landscape type on colony weight in a full model using data from both 2016 and 2017 ($F_{3,9.08} = 2.2$, $p = 0.15$). However, there were significant effects of year ($F_{1,121.1} = 27.4$, $p < 0.001$), assessment period ($F_{5,120.09} = 3.75$, $p = 0.003$), the interaction of landscape and year ($F_{3,121.08} = 5.4$, $p = 0.001$), and the interaction of year and assessment period on colony weight ($F_{5,120.09} = 1.37$, $p = 0.003$). In 2016, overall average colony weight in suburban landscapes was 45-46% lighter than those in organic agriculture and natural landscapes (Post-hoc: $p = 0.05$ and $p. = 0.05$, respectively, Figure 2A.). Additionally, colonies in suburban landscapes were 52% lighter than those in natural landscapes ($p = 0.02$) in assessment period three, 61% lighter than both organic ($p < 0.001$) and natural ($p < 0.001$) landscapes in assessment period four, and 61-65% lighter than all three landscape types (conventional: $p = 0.008$; organic: $p = 0.009$; natural: $p = 0.002$) in assessment period five (Figure 2A). Overall, differences in average colony weight between agricultural and natural landscapes in 2016 were only within 2-4%, resulting in no statistical significance ($p > 0.9$ for all). Suburban landscape colonies in 2017 followed a similar trend to those in the previous year (21-26% lighter than the other landscape types) Though, we found no significant differences in overall colony weight and in any assessment period ($p > 0.6$ for all).

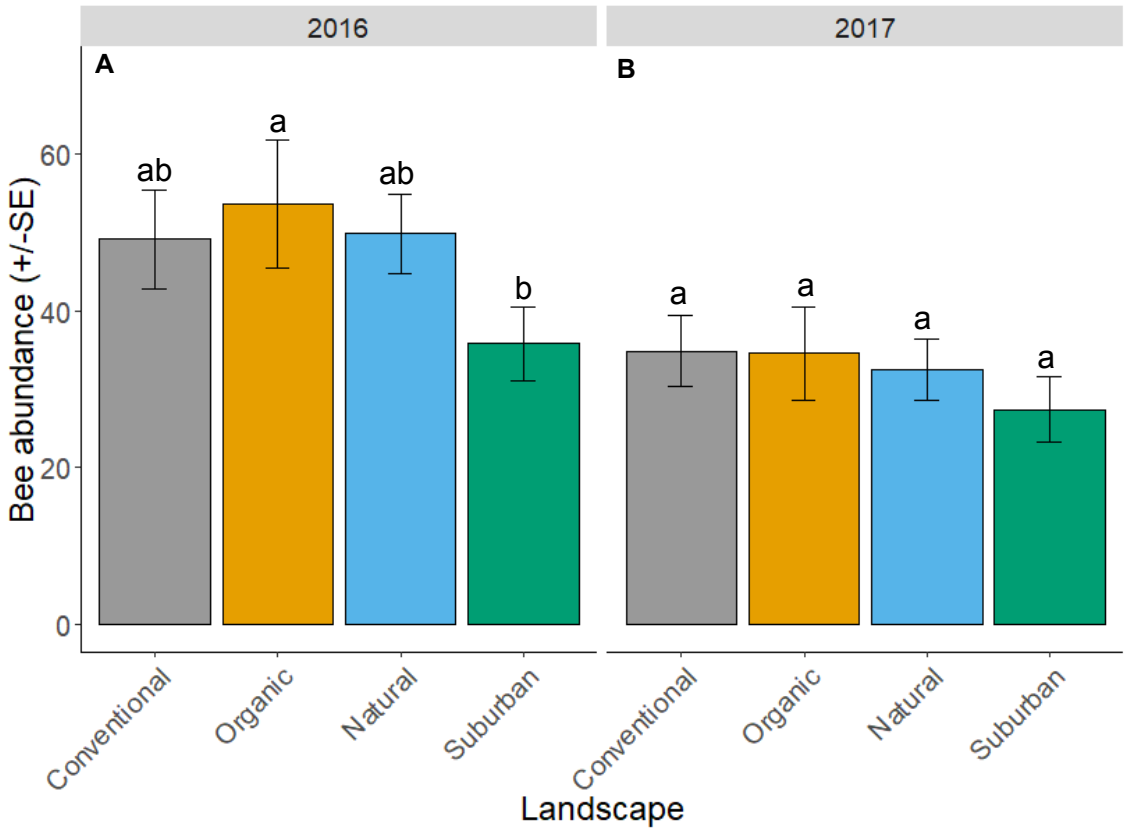

Figure 3. Mean bee abundance in (A) 2016 and (B) 2016 for colonies of *B. impatiens* placed in agricultural, natural and suburban landscapes. Letters above error bars indicate significant differences between landscape based on post-hoc tests of lme models.

Bee abundance **–** There was a significant effect of year, assessment period and the interaction between landscape and year on bee abundance ($F_{1,121.57} = 136.3$, $p < 0.001$; $F_{5,120.14} = 12.6$, $p < 0.001$; $F_{3,121.53} = 3.06$, $p = 0.03$, respectively). Suburban landscapes on average had significantly fewer bees in their colonies than organic agriculture landscapes (34% reduction; Figure 3A 2016, $p = 0.04$). In 2016, suburban landscapes had 40-45% fewer bees in their colonies compared to both agricultural landscapes (conventional: $p = 0.03$; organic: $p = 0.008$) in assessment period four and 53-55% fewer bees than all landscape types conventional: $p = 0.01$; organic: $p = 0.002$; natural: $p = 0.006$) in assessment period five. Differences in bee abundance

between agricultural and natural landscapes were only within 2-7% in 2016 ($p > 0.1$ for all). There were no significant differences between any landscape types in 2017 ($p > 0.4$ for all).

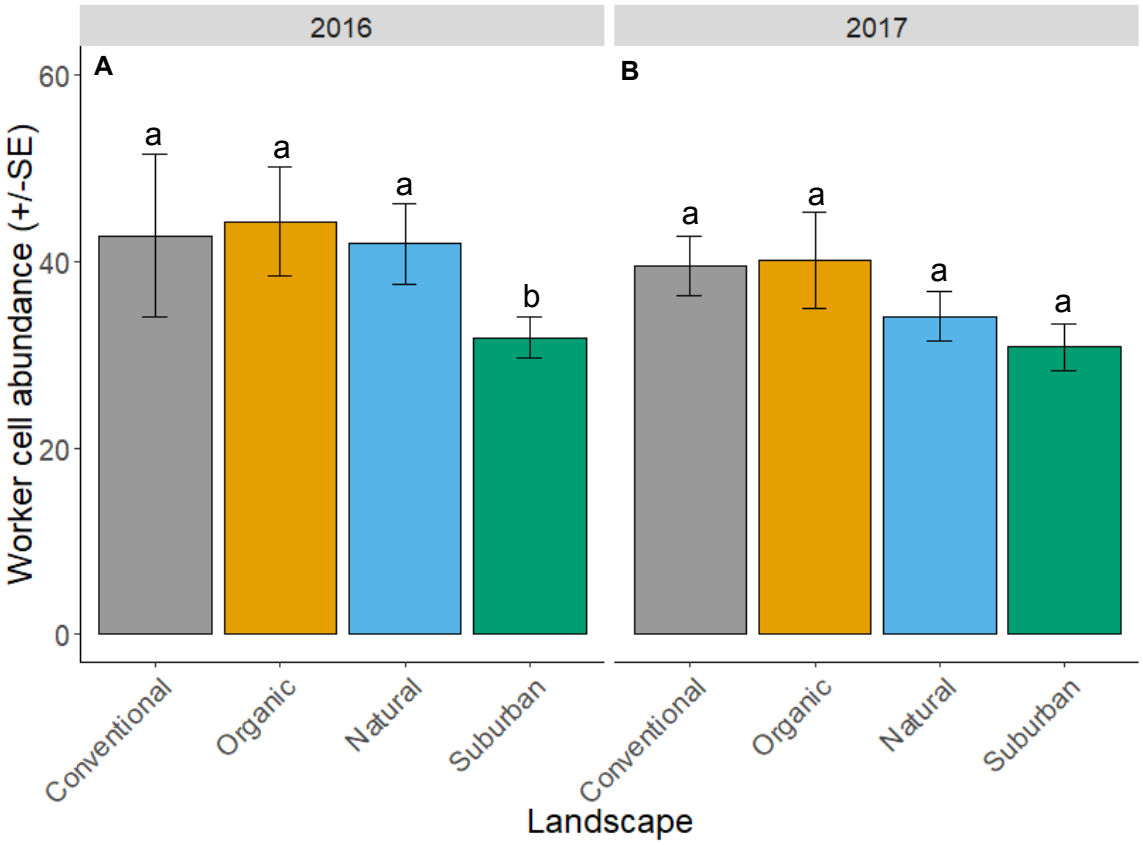

Figure 4: Mean worker cell abundance for colonies of *B. impatiens* placed in agricultural, natural and suburban landscapes in (A) 2016 and (B) 2017. Letters above error bars indicate significant differences between landscape based on post-hoc tests of lme models.

Worker cell abundance – Worker cell abundance was significantly impacted by landscape type ($F_{3,9.10} = 5.58$, $p = 0.01$), year ($F_{1,122.46} = 31.79$, $p < 0.001$), period ($F_{5,120.05} = 4.51$, $p < 0.001$), and the interaction between year and period ($F_{5,120.04} = 8.2$, $p < 0.001$). In 2016, suburban landscape colonies produced over 50% fewer worker cells than the other landscape types (Figure 4A 2016, conventional: $p = 0.003$; organic: $p = 0.01$; natural: $p = 0.01$). During weekly visits, suburban landscapes had 60% fewer worker cells than natural landscapes in assessment three, 64-74% fewer worker cells between all landscape types in assessment period

four (conventional: $p = 0.002$; organic: $p = 0.001$; natural: $p = 0.001$) and five (conventional: $p < 0.001$; organic: $p = 0.01$; natural: $p < 0.001$), and 75% fewer worker cells than conventional agriculture landscapes in assessment period six ($p = 0.02$). There were no significant differences in worker cell abundance between natural landscapes and both agricultural landscapes in 2016 ($p > 0.9$ for all) and no significant differences between any landscape types in 2017 ($p > 0.1$ for all).

Colony fitness and survival

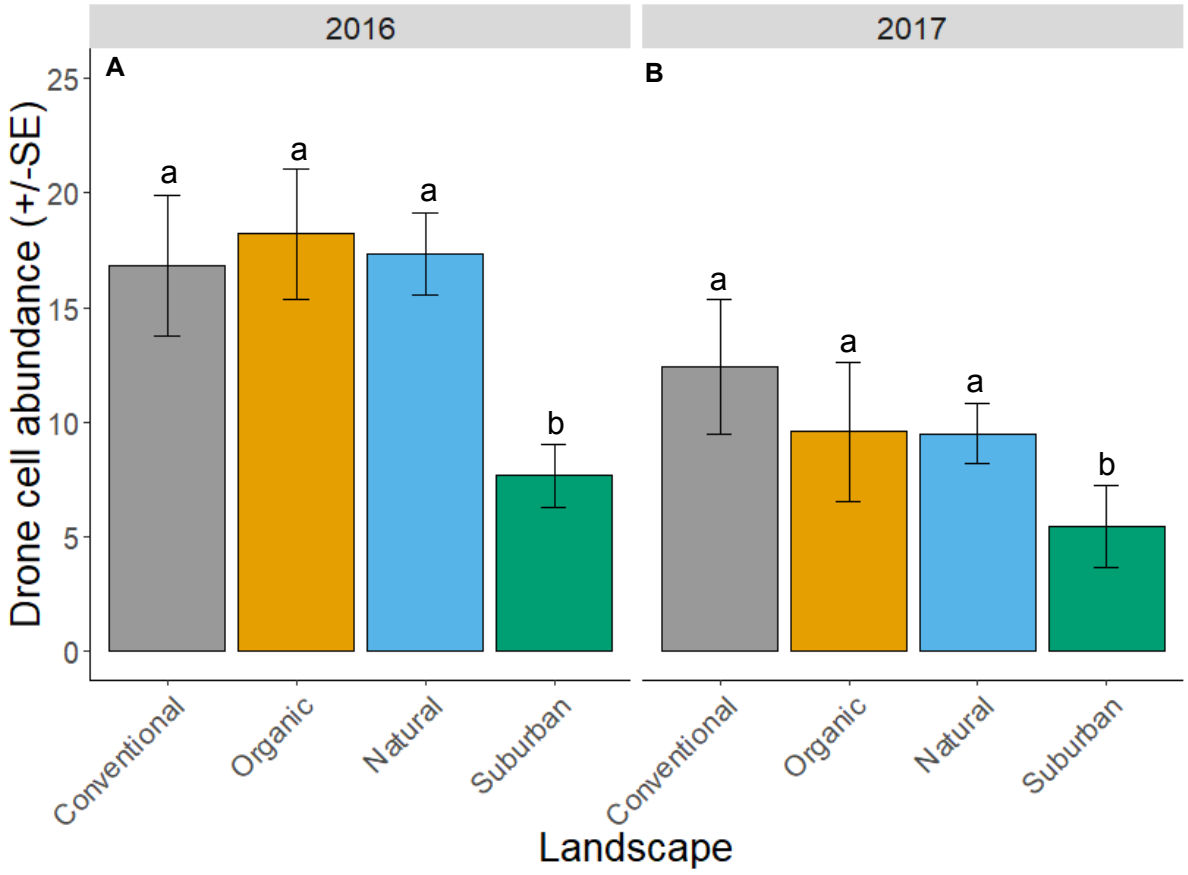

Figure 5: Mean drone cell abundance (+/- SE) in (A) 2016 and (B) 2017 of *B. impatiens* colonies placed in agricultural, natural and suburban landscapes. Letters above error bars indicate significant differences between landscape based on post-hoc tests of lme models.

Drone cell abundance – We found a significant effect of landscape ($F_{3, 9.24} = 3.62$, $p = 0.05$), year ($F_{1,122.46} = 36.03$, $p < 0.001$), period ($F_{5,120.25} = 9.59$, $p < 0.001$), the interaction of landscape and year ($F_{3,122.33} = 3.14$, $p = 0.02$), and the interaction of year and assessment period ($F_{5,120.25} = 2.84$, $p = 0.01$) on drone cell abundance. Overall, suburban landscapes colonies had 53-55% fewer drone cells than the other three landscape types (Figure. 5A, conventional: $p < 0.05$; organic: $p = 0.01$; natural: $p < 0.02$). Furthermore, suburban landscape colonies had 65% fewer drone cells than organic ($p = 0.03$) and natural ($p = 0.02$) landscapes in assessment period three and 82-84% fewer drone cells than all three landscapes types (conventional: $p < 0.01$; organic: $p = 0.05$; natural: $p < 0.02$) in assessment period five. There were no significant differences in drone cell abundance between natural landscapes and both agricultural landscapes in 2016 ($p > 0.9$ for all) and no significant differences between any landscape types in 2017 ($p > 0.1$ for all).

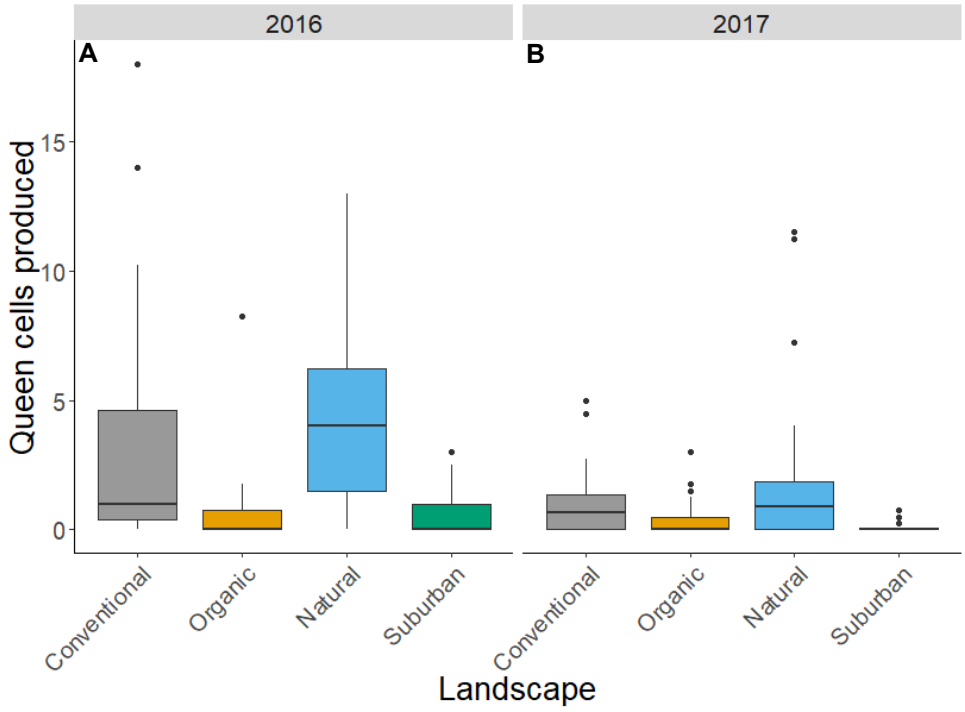

Figure 6: Queen cell production in (A) 2016 and (B) 2017 of *B. impatiens* colonies placed in agricultural, natural and suburban landscapes.

Queen cell and gyne abundance *–Bombus impatiens* colonies in suburban and organic landscapes had the least virgin queen cell abundance (Figure 6A and B). Conversely, conventional agriculture and natural landscapes produced on average 45-57% more queen cells than organic agriculture and suburban landscapes in 2016 and 2017. Yet, there were no overall significant differences in the binomial presence/absence model. In the hurdle model, virgin queen cells in suburban and organic colonies were twice as likely of not being observed (Figure. S1; suburban: $p = 0.02$, organic: $p = 0.01$). This in turn resulted in a similar pattern in gyne abundance (Figure S2; suburban: $p < 0.01$).

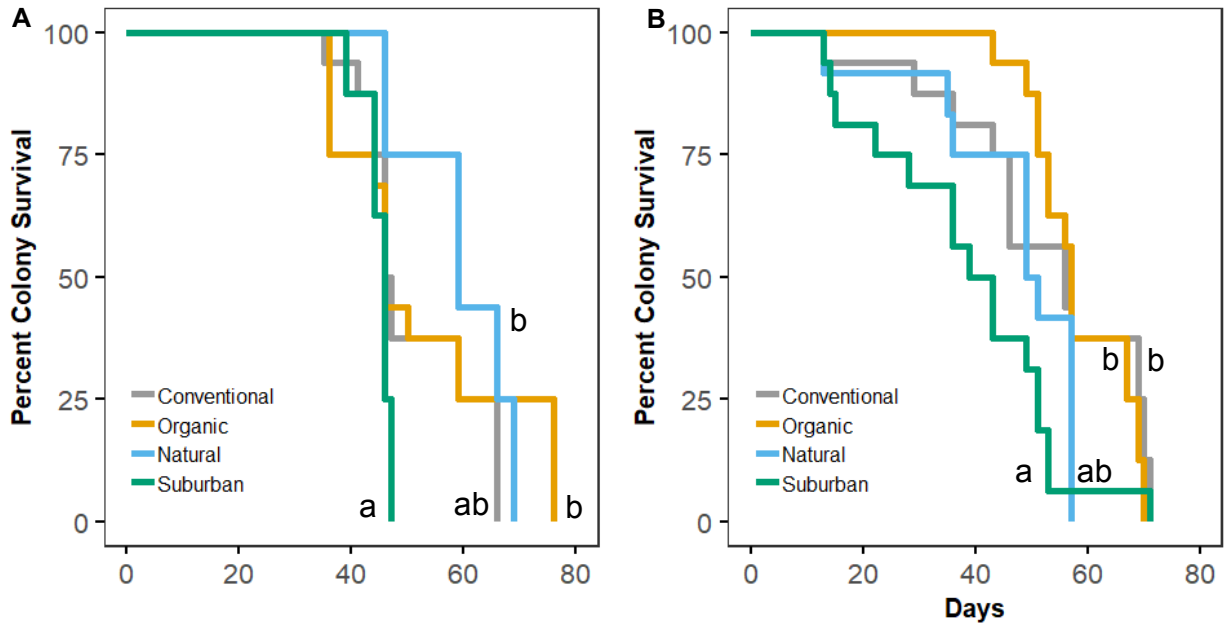

Figure 7: Kaplan-Meir curves representing the number of days colonies spent in the field before queens died (A) 2016 and (B) 2017. Each step in the Kaplan-Meier survival curves represents the day when a queen died resulting in the removal of the colony from the experiment. Letters indicate significant differences between landscapes based on post-hoc tests of Cox proportional hazard models with mixed effects.

Colony survival. Data collection for each colony was terminated when the queen died. In both years, suburban landscape colonies were likely to experience queen death at a rate two times greater than the colonies in the other landscape types (Hazard Ratio = 2.46, $p = 0.001$). In

2016, colonies survived in the field for an average of fifty-two days. All of the suburban landscape colonies were removed six days earlier than the overall average lifespan (Figure. 7A). A post-hoc test showed that survival time of queens in suburban landscapes were significantly different than those in organic agriculture landscapes and natural landscapes. (Figure: 7A, $p < 0.01$ and $p < 0.01$, respectively). In 2017, colonies in suburban landscapes had longer lifespans (Figure: 7B). However, over fifty percent of the colonies were removed from the study before the overall average lifespan of 49 days. Post hoc tests showed that survival time in suburban landscapes were significantly different in comparison to both conventional and organic agriculture (Figure: 7B, $p = 0.019$ and $p = 0.012$, respectively).

Predictors of colony performance, fitness and survival

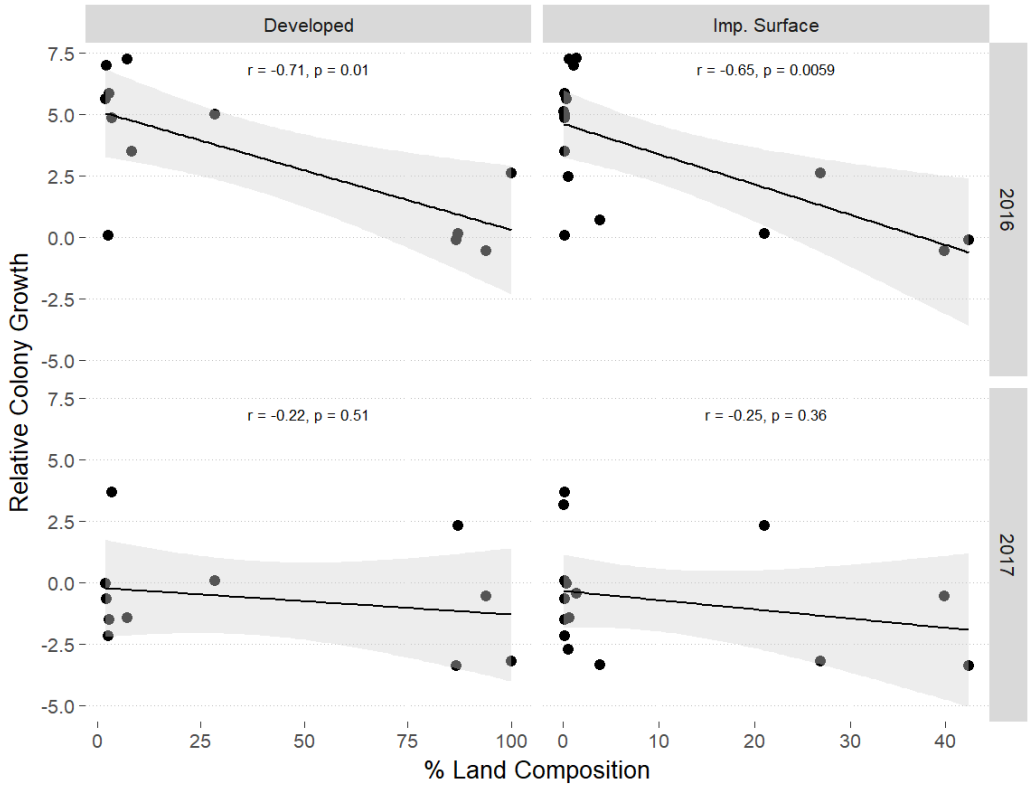

Figure 8: Correlations depicting the relationship between daily relative colony growth of *Bombus impatiens* colonies until assessment period four and percent land composition developed land and impervious surface in 2016 and 2017. Correlation method used: Pearson's.

As a first step towards assessing why colonies in some landscapes performed worse than others, we tested for quantitative relationships between performance and landscape characteristics. Pearson's correlation coefficients were computed to examine relationships between relative colony growth and percent agricultural land, natural land, developed land, impervious surface, and temperature at assessment period four in 2016 and 2017. In 2016, there was a significant negative relationship between relative colony growth and increasing developed land and impervious surface (Figure: 8: developed n = 16, R = -0.71, p = 0.01; impervious n = 16, R = -0.65, p = 0.006). We found no significant differences between relative colony growth and both agricultural and natural lands in 2016 and 2017 (Figure S4). There were significant negative relationships between bee abundance and increasing percent developed land and impervious surface in 2016 (Figure. S5A: developed n = 16, R = -0.54, p = 0.03; impervious n = 16, R = -0.53, p = 0.036). Worker cell abundance was significantly negatively correlated with increasing developed land and impervious surface in both 2016 (Figure. S5B: 2016, developed n = 16, R = -0.62 p = 0.01; impervious n = 16, R = -0.6, p = 0.015) and 2017 (Figure. S5B: 2017, developed n = 16, R = -0.56, p = 0.03; impervious n = 16, R = -0.61, p = 0.016).

Drone cell abundance was significantly negatively correlated with increasing developed land and impervious surface in 2016 (Figure. S6A: 2016, developed n = 15, R = -0.67 p = 0.004; impervious n = 15, R = -0.63, p = 0.008) and only impervious surface in 2017 (Figure. S6A: n = 15, R = -0.54, p = 0.036). Queen cell abundance was only significantly positively corelated with increasing agricultural land composition in 2016 (Figure S6B: n = 16, R = 0.66, p = 0.005).

There were no significant relationships between relative colony growth and land composition in 2017 (Figure 4 and Figure. S4). There were also no significant relationships between relative colony growth and temperature in both 2016 and 2017 (Figure S7).

Discussion

Few studies have attempted to compare contrasting landscapes and land management practices, such as conventional and organic farm practices, natural landscapes, and urban/suburban landscapes on bumble bee colony performance and fitness. In 2016, colonies in suburban landscapes experienced the least weight gain, had the least number of bees present in colonies, and produced the least number of worker cells, drone cells, and queen cells. Additionally, colonies in suburban landscapes had an average lifespan 15-25% shorter than the other landscapes. Although we saw no overall significant differences in colony performance between landscapes in 2017, suburban landscapes followed a similar trend by experiencing the least weight gain, bee abundance, and brood production. They also had 20- 34% shorter lifespans than those in the other landscape types. Contrary to our expectations, we saw no significant differences in colony weight between agricultural landscapes and natural landscapes in in both years of the study, suggesting that the surrounding landscape context may be explaining the variation or lack thereof between landscapes rather than agricultural management practices.

The percent natural area surrounding the agricultural and natural landscape sites may explain why bumble bee performance was best at these sites and why we didn't see significant differences between the three landscape types. Agriculture lands in New York State, whether the practice is conventional or organic, are surrounded by some degree of natural habitat. In this study, the percent of natural land surrounding both agricultural landscapes were relatively the same (Figure 1). However, provided that conventional agriculture and natural landscapes both produced greater amounts of virgin queen cells than organic agriculture landscapes (Figure 3), this suggests that there may be variability in the quality and abundance of resources present at the farms and in the surrounding natural landscape (Spiesman et al. 2017). Potentially, with

greater amounts of floral resources, bumble bee colonies will switch to production of queen cells (Plowright and Pendrel 1977, Pomeroy and Plowright 1982, Duchateau and Velthuis 1988). This finding would be consistent with research demonstrating the benefits of agricultural fields surrounded by natural habitat and enhanced with wild flower strips as supplemental forage for wild pollinators (Pywell et al. 2005, Pywell et al. 2006, Garibaldi et al. 2014, Williams et al. 2015). Alternatively, a large continuous crop production during the summer months such as the cucurbit production found in the conventional agriculture landscapes could be beneficial during dearth periods of wild floral resources (Williams and Kremen 2007).

Results from our suburban landscape colonies suggest that the suburbs are a subpar habitat for bumble bees. Suburban landscape colonies experienced the least growth, caste production, and shortest lifespans. In addition, most performance metrics were significantly negatively correlated with increasing developed land and impervious surface in both years. Recent publications have demonstrated varying results in bumble bee performance in response to urban landscapes. For example, Samuelson et al. (2018) found that colonies placed in the "city" and "village" had greater peak sizes, bee abundance, and production of sexuals than agricultural landscapes, which is consistent with other studies performed in the United Kingdom highlighting the positive impacts of suburban gardens (Goulson et al. 2002, Goulson et al. 2010). In North America, Vaidya et al. (2018), found no significant performance differences in *Bombus impatiens* colonies placed in gardens across an urbanization gradient in and around Detroit, MI, USA. It is plausible that larger amounts of floral resources in suburban and urban gardens are mitigating any negative impacts generally associated with urbanization in the studies above (Goulson et al. 2002, McFrederick and LeBuhn 2006, Goulson et al. 2010). However, because we know that urban landscapes can have both positive (McFrederick and LeBuhn 2006) and

negative (Glaum et al. 2017) impacts on bumble bee diversity and abundance, it may simply be that some bumble bee species are more tolerant than others to the effects of urbanization and that there are regional differences even within the same species.

Floral resource data, pesticide use patterns, and incidence of bumble bee pathogens were not assessed in our study. Knowledge of how these factors impact *B. impatiens* could explain why colonies performed poorly in suburban landscapes and why there were little to no differences in colony performance and survival between agricultural and natural landscapes (Potts et al. 2010, Winfree et al. 2011). Lack of floral resources (sufficient, diverse and appropriate sources), pesticide exposure, pathogen exposure and climate change can reduce longevity and growth of bee populations (Maurizio and Hodges 1950, Frias et al. 2016, Lentola et al. 2017). These stressors often co-occur and can be more harmful to bees during simultaneous exposure than on their own (Brown et al. 2000, Riddell and Mallon 2006, Pettis et al. 2013, Gill and Raine 2014).

While our suburban sites indeed had flowering ornamental plant species in both front and back lawns, the quality of these resources pertaining to *B. impatiens* fitness and survival is not known. Potentially, homeowners are not purchasing appropriate plant species for pollinators visiting their gardens. Campbell et al. (2017), showed that 46% of homeowners choose pollinator-friendly plants primarily on attractiveness rather than their benefits for pollinator species (but see Garbuzov and Ratnieks 2014). In addition, some pollinators such as bumble bees exhibit flower constancy (Free 1970), suggesting that having many flower types in a garden may make it difficult for them to switch between multiple plant species while foraging (Gegear and Laverty 1998, Goulson 2000). If local floral resources are lacking, bumble bees may fly to surrounding natural habitats for adequate forage (Spiesman et al. 2017). Provided that the

suburban sites used in this study had an average of 6% natural land composition in the surrounding landscape (Figure: 1B), foragers would have had to travel further than their average flight distance to collect nectar and pollen, which could be detrimental to colony success (Osborne et al. 2008). Though the results were not significant, a positive trend of colony relative growth with increasing natural land (Figure: S2) may indicate that colonies in agricultural and natural landscapes are utilizing resources in those areas when they are available.

Exposure to pesticides have been widely documented in agricultural landscapes (Mullin et al. 2010, Lambert et al. 2013, Pettis et al. 2013, Hladik et al. 2016) and can impair foraging behavior (Gill and Raine 2014), reduce colony growth, and reproduction in bumble bees (Gill et al. 2012, Rundlöf et al. 2015). Pesticide exposure in urban landscapes are less understood, but there is evidence of low pesticide exposure to bumble bees in suburban landscapes (David et al. 2016, Botías et al. 2017). Four of our agricultural landscapes used conventional farm practices, which indicates that exposure to pesticides in those sites is highly likely. Although, because conventional agriculture colonies performed just as well or better compared to organic agriculture and natural landscapes (presumed little to no exposure to pesticides), another mechanism may be mitigating the impacts of pesticides at those sites (i.e. floral resources). Given that common pesticides used in agricultural fields and home lawns (i.e. imidacloprid, thiamethoxam and glyphosate) can be found far from the point of application (Goulson 2013, Herbert et al. 2014), this allows for indirect exposure to pesticides between different landscape types, especially in urban/suburban landscapes. This may be a potential route for pesticide exposure in the suburban landscapes in this study. Future studies will benefit from conducting pesticide residue analyses of bees and nest wax to determine pesticide exposure variation across different landscape types.

Pathogen and parasite exposure can reduce overall colony performance, increase mortality, and reduce reproductive mortality (Imhoof and Schmid-Hempel 1999, Yourth et al. 2008, Graystock et al. 2016) and there is wide evidence attributing this to landscape context (Goulson et al. 2012, Theodorou et al. 2016, McArt et al. 2017). In addition, these impacts can be exacerbated when combined with poor nutrition and/or pesticide exposure (Brown et al. 2000, Pettis et al. 2013, Fauser-Misslin et al. 2014). Pollen protein content (Tritschler et al. 2017) and plant secondary compounds (Biller et al. 2015, Richardson et al. 2015) can govern how bees handle pathogen infection. In this study, any potential negative physiological impacts of pathogen infection may have been relieved in colonies placed in agricultural and natural landscapes because of potentially greater floral resources in the surrounding environment. Conversely, colonies in suburban landscapes would have been more prone to pathogen infection because floral resources are often found in concentrated patches where many bees will congregate and share resources, increasing chances of pathogen transmission (Durrer and Schmid-Hempel 1994, Goulson et al. 2012, Theodorou et al. 2016).

Both percent impervious surface and developed land were strongly negatively correlated with relative colony growth and primarily driven by the suburban landscape sites (Figure: 8). Urban landscapes have not only been shown to negatively impact pollinator densities and diversity via habitat degradation but also interact with warming temperatures. Hamblin et al. (2018) demonstrated that bee abundance decreased by 41% with each average increase in degree Celsius per site despite floral abundance. During warm conditions, bumble bees may undergo physiological challenges. Their morphology makes them susceptible to overheating (Oyen et al. 2016) and in some cases workers may switch from foraging to fanning, resulting in reduced resource intake and increased stress (Vogt 1986). At our sites, we saw no relationship between

average daily temperatures and relative colony growth at assessment period four (Figure. S7; 2016: $n = 16$, $R = 0.19$, $p = 0.13$; 2017: $n = 15$, $R = 0.094$, $p = 0.047$) and no relationship between average daily temperature and land composition (Figure. S8). However, compared to the agricultural and natural landscape sites, suburban sites may have had greater exposure to direct sunlight due to limited sources of full shade in homeowner backyards. In 2016, much of northeastern United States, including New York experienced one of the warmest and driest summers in 60 years (Sweet et al. 2017). In addition to directly impacting bumble bees via heat stress, the drought would have had indirect effects by reducing nectar flow and pollen production of nearby plants (Scaven and Rafferty 2013). In agricultural landscapes and natural landscapes, these impacts may have been mitigated using irrigation systems for crops and small bodies of water (i.e. streams and creeks), respectively. Although, more precipitation occurred in 2017, there is no reason to suggest that it influenced colony growth given the decline across all sites (Figure 2B).

In conclusion, research on how landscape shapes pollinator diversity, abundance, performance, and fitness is important for determining how best to conserve pollinators. Multiple stressors in various landscape contexts, especially when they occur simultaneously, can strongly impact pollinator health and populations (Winfree et al. 2011, Goulson et al. 2015). The research presented here is one of few studies comparing both multiple land management practices and landscapes. Furthermore, we demonstrated that suburban landscapes were not conducive for *B. impatiens* colonies and conversely so in conventional agriculture. Such results warrant further exploration of these landscapes to determine the mechanisms influencing bumble bee colony dynamics and to better advise conservation efforts of bumble bee species and their populations.

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